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# FLOW-ASSISTED MANTLE CAVITY REFILLING IN JETTING SQUID

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## ABSTRACT

During rapid, rearward, repetitive jetting, the mantle of a squid is expanded laterally by hydrodynamic pressure differences between the region of greatest girth and the refilling apertures beneath its downstream margin; this flow-induced expansion assists refilling between jet pulses. Estimates derived from measurements of pressure distributions on a model in wind tunnels indicate that about 50% of the pressure available for refilling is flow-induced at a speed of 3 $\mathrm{m \cdot s^{-1}}$ while 90% is flow-induced at 9 $\mathrm{m \cdot s^{-1}}$.

## INTRODUCTION

Rapid rearward (dorsally directed) locomotion in squid is accomplished by ejection of water from the mantle cavity through a ventrally directed funnel. The cavity then refills through a bilateral pair of one-way valves at the anterior end of the mantle, and the ejection process may be repeated. While clearly less efficient than the swimming of fish (O'Dor, 1982), this jet propulsion system is capable of propelling animals at impressively high speeds at least in brief episodes.

Refilling the mantle cavity demands that the mantle expand its circumference, no ordinary activity for a muscular organ. Two mechanisms have been recognized as contributing to the expansion. Ward and Wainwright (1972) drew attention to a set of very short radial muscle fibers within the mantle, whose contraction could thin the mantle and extend the circumferential muscles. Gosline and Shadwick (1983) showed that, in addition, elastic storage of energy from the expulsion phase played a significant role early in the process of re-expansion.

An additional agency for refilling may be involved, a consequence of the pressure distribution predicted by Bernoulli's principle. If a spherical or ellipsoidal body moves through a fluid, a characteristic distribution of pressures develops along its surface, with the most subambient pressures occurring near or ahead of the region of maximum cross-sectional area normal to flow. If the body is reasonably streamlined (as is a squid), flow follows its surface, moving downstream without substantial separation or reversal, and pressures rise again behind the widest portion. For a jetting squid, maximum girth is adjacent to mantle and mantle cavity; the openings between mantle margin and neck through which refilling occurs are well downstream. Thus pressure inside the mantle cavity should be higher than that outside, creating a net outward force that might augment the actions of radial muscles and elastic connective tissue. [The possibility was mentioned by Ward (1972) but was regarded as inconsequential inasmuch as squid could refill adequately in still water.]

Such flow-induced pressures might reduce the time needed to refill or increase the volume of water in the mantle cavity prior to ejection. Indeed, rapidly moving squid appear to pulse more frequently than those constrained to remain at rest with respect

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to the local water (Gosline, pers. comm.). Functional roles of analogous flow-induced pressures have been previously investigated in fish (DuBois *et al.*, 1974), in an alga (Vogel and Loudon, 1985), and in scallops (Vogel, 1985).

Unfortunately, squid have never been persuaded to perform high speed escape responses with repetitive jetting in any form of confinement. Furthermore, their soft-bodied character, especially when dead, precludes direct measurement of pressures as was done with fish and scallops. Instead, the present study makes recourse to a somewhat abstract physical model—a radially symmetrical body of revolution with a lengthwise row of surface apertures for measurements of the distribution of pressures. Pressures determined on the model are compared to those generated by previously described refilling mechanisms to estimate the contribution of flow-induced pressure differences to the overall process.

## MATERIAL AND METHODS

The model squid (Fig. 1, top) was based on measurements abstracted and averaged from a variety of published and unpublished photographs giving lateral views of *Loligo,* mostly *L. pealei.* Few pictures showed animals in motion, and all reflected full or nearly full mantle cavities. Fins were omitted in the model since they are apparently folded flat against the mantle during rapid jetting (Bradbury and Aldrich, 1969; William Kier, pers. comm.). The extent to which the ventral margin of the mantle hooded the head and the smoothness of fairing of mantle and head varied among the photographs; the model assumes a small head, poor fairing, and little hooding—in short, a worst case from the point of view of smooth flow. [It should be noted that Bradbury and Aldrich (1969) showed an unusually conspicuous gap, nearly that of the present model, between mantle margin and head during refilling in *Illex illecebrosus.*] At the same time, the model permitted "improvement" through the addition of modelling clay.

The model, of aluminum, was 293 mm in length and 50 mm in maximum diameter. Squid are nearly circular in cross-section; the use of a radially symmetrical model is thus only mildly abnormal. Radial symmetry permitted simple fabrication on a lathe and radically reduced the number of measurements needed to map pressure distributions. Thus a single lengthwise row of 24 holes sufficed; these were 10 mm apart in lateral projection, beginning 10 mm behind the upstream (dorsal) end. Each was normal to the surface, 1 mm in diameter, and penetrated to an axial hole running downstream to an exit within the "arms." An additional hole entered the model between head and mantle margin. For pressure measurements all but one of these apertures were occluded by small pieces of plastic adhesive tape. The model was supported by a cylindrical tube that continued the axial hole downstream and by a cylindrical support beneath the widest part of the mantle, diametrically opposite the row of holes.

Pressure measurements were made in air at speeds of 8.75, 16.5, 37.3, and 76.7 $m \cdot s^{-1}$, the lower speeds in the large open circuit tunnel of the Department of Zoology (Duke University) and the higher speeds in the closed circuit tunnel of the School of Engineering. All were differential measurements referred to a static aperture, 1 mm in diameter, 0.1 m downstream from the leading edge of a flat plate parallel to flow that was mounted adjacent to the model.

Where neither compressibility of fluids nor fluid-fluid interfaces complicate matters, the choice of fluid and size of model are quite arbitrary as long as the natural value of the Reynolds number is maintained. Equality of Reynolds number (Re) between reality and model assures dynamic similarity of flows and thus equality of the dimensionless force and pressure coefficients, as discussed by Vogel (1981), Vogel and Loudon (1985), and standard texts in fluid mechanics. Shifting from 20°C seawater to air entails a speed increase factor of 14.5; the use of a model 1.5 times larger than an assumed size of animal mandates a speed decrease of this latter factor. Thus the present speeds in air are functionally equivalent to speeds of 0.91, 1.6, 3.9, and 7.9 $\mathrm{m \cdot s^{-1}}$ in seawater providing that pressures are expressed as pressure coefficients. (A pressure coefficient is simply the measured pressure difference divided by the dynamic pressure, the latter being the product of half the density of the medium and the square of the velocity. In practice, pressures were coverted to the coefficients using the density of air and the tunnel velocities; the coefficients were reconverted as needed to equivalent pressures in seawater by substituting the density of seawater and the corresponding speeds in water.)

Pressure differences were measured with a barocell electric manometer and capacitative differential pressure sensor (Datametrics-Dresser, 1174-B1A-5A1-A1 and 570D-10T-2A1-V1X). The combination had a maximum capacity of 1300 Pa and an accuracy, according to the manufacturer, of better than 0.13 Pa (in practice better than any locally available standard). This accuracy corresponds to a pressure coefficient of less than 0.003 for all present measurements. Tunnel speeds were determined with a Pitot-static tube, 3.2 mm in diameter (United Sensor, Inc., PCC 12-KL) and the same barocell and sensor except for the highest speed, for which a simple water manometer (readable to 0.2 mm) provided the necessarily wider range.

Pressure drag (total drag less skin friction) can be viewed as a summation of the streamwise-directed components of the pressures on the surface of a body, where each datum for pressure has been multiplied by the area of surface to which it applies. If skin friction is negligible, it is thus a simple matter to derive values for drag from the pressure measurements; these drag data can be converted to drag coefficients in a manner analogous to the conversion of pressures to pressure coefficients (Vogel, 1981). Thus a general test of procedure and apparatus was carried out by determining the pressure distribution around circular cylinders and from the latter computing drag coefficients—values of 1.0 were obtained at Reynolds numbers of 8000 and 32,000; a commonly cited value is 1.1 (Hoerner, 1965), of which about 3% is skin friction. Similarly, a sphere at Re = 28,000 gave a drag coefficient of 0.42; the accepted value is 0.47.

## RESULTS

### *Pressure coefficients*

Figure 1 (bottom) gives pressure coefficients as a function of position for the model squid. Several points are noteworthy.

(1) These curves are typical of results obtained for streamlined objects (see Discussion). They vary little with changes in Reynolds number (proportional to speed) although the minimum pressure coefficients are slightly more negative at higher Reynolds numbers. Thus the model is well-streamlined—if the decrease in girth is appropriately gentle as flow moves downstream from the point of maximum width then little separation of flow occurs; irregularities further downstream (unfaired mantle margin, head, and arms) are of little consequence. In fact, building up the head area with modeling clay had so little effect that no systematic exploration was made.

(2) The minimum pressure coefficients occur well downstream, not inevitably the case for streamlined bodies of revolution. Clearly location of the pressure minimum near the point of maximum girth will be advantageous for flow-induced refilling of the mantle cavity.

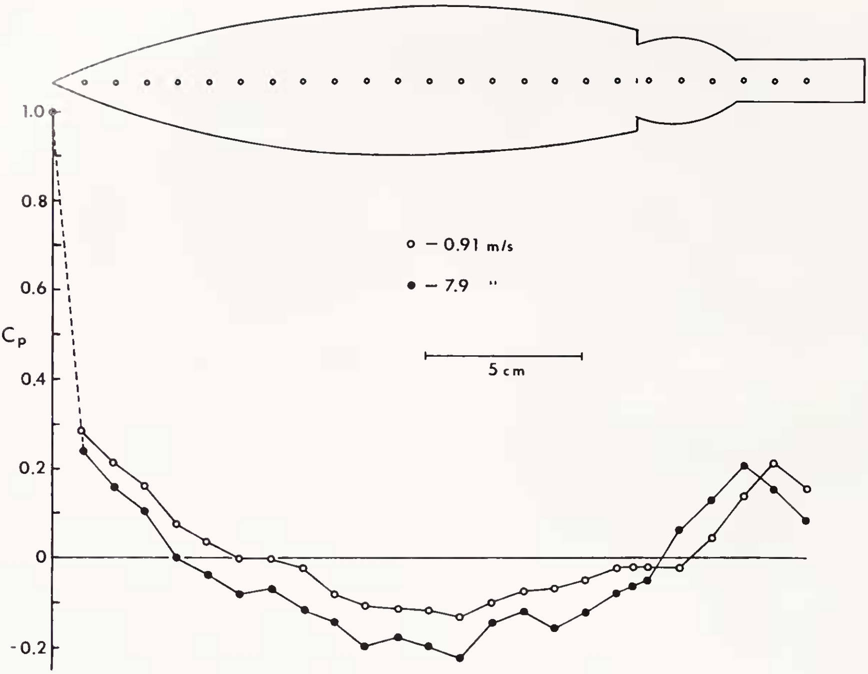

FIGURE 1. Top: the model squid, with flow from left to right, showing location of the apertures for measurement of pressure. Bottom: pressure coefficient ($C_p$) as a function of relative distance downstream from the dorsal extremity; the abscissa is scaled to correspond to the drawing above. Extrapolation to a coefficient of unity at the upstream extremity (dotted line) presumes the existence of a normal forward stagnation point. Speeds refer to equivalent values in seawater; all data for the two intermediate speeds fall between those shown for the maximum and minimum speeds.

(3) The pressure coeffients for the mid-mantle region are about −0.15 while those for the region around the head from which refilling must take place are about +0.10; a difference of approximately 0.25 is thus available for refilling the mantle cavity. The corresponding pressure differences in seawater for the four speeds tested are 106, 330, 1950, and 8000 Pa. (The wide range of these latter figures reflects multiplication by the squares of the velocities to obtain pressures from the pressure coefficients.)

### *Pressure drag*

While not directly germane to the present hypothesis, values for pressure drag emerge from these measurements of pressure. Expressed as drag coefficients for the four speeds tested, the latter are (in ascending order of speed) 0.070, 0.060, 0.027, and 0.033, all referred to frontal (maximal cross-sectional) area. Dividing these values by 13.6 (the ratio of total surface to frontal area) shifts the reference to total surface or "wetted" area. Dividing the values instead by 2.13 (the ratio of volume to the two-thirds power, a nominal area, to frontal area) shifts the reference to $V^{2/3}$.

These coefficients are about an order of magnitude below those of cylinders and spheres, cited earlier. There is no obvious discontinuity in the data corresponding to the drop in pressure drag attending the delay of separation as the boundary layer becomes turbulent (Vogel, 1981). Both these features of the data indicate good streamlining with little separation and low total drag for the model. If this crude model gives such a good account of itself then it is likely that real squid moving rearward are well-streamlined.

## DISCUSSION

Evaluation of the contribution of flow-induced pressure differences to mantle cavity refilling requires two further items of information: (1) the pressure available for refilling in the absence of any direct hydrodynamic effect and (2) the speeds at which squid move during rearward repetitive jetting.

Three separate approaches to estimating the non-hydrodynamic pressure available are currently practical. First, a very rough upper limit is suggested by the capability of the radial muscle of the mantle. The latter underlies about 10% of the mantle surface (Bone *et al.*, 1981); such muscle should be capable of a stress output of 100 $kN \cdot m^{-2}$ in the non-isometric contraction by which the mantle wall is thinned, or 10 $kN \cdot m^{-2}$ referred to mantle area instead of muscle cross-section. Half of the output will be lost since the mantle cannot expand longitudinally, leaving 5 $kN \cdot m^{-2}$ or 5000 Pa. Indeed, this figure may considerably exaggerate what the muscle can do in the latter part of mantle expansion when it is already substantially contracted. And it is in this hyperexpansion phase that the elastic recoil with which mantle expansion begins is no longer significant (Gosline and Shadwick, 1983). Conversely, at near maximum expansion, flow-induced pressures should be greatest.

Second, from observed rates of refilling in non-swimming squid together with the size of the openings through which refilling occurs, Trueman (1980) calculated an inhalent pressure of 1200 Pa. And third, rough but direct measurements of peak refilling pressures are given by Trueman (1980) as 1500 Pa and by Gosline and Shadwick (1983) as 1000 Pa.

More problematical are the speeds attained by swimming squid during the rearward bursts of repetitive jetting. The animals are notoriously ill-adapted to survive in any non-pelagic situation (Summers and McMahon, 1974); and high-speed, repetitive jetting seems never to have been elicited under controlled and reproducible circumstances. Johnson *et al.* (1972) and Trueman (1975) calculated a speed of 3.5 $m \cdot s^{-1}$; but the value is based on the drag coefficient of a sphere (0.47), certainly much too high for a well-streamlined form. Replacing this assumption with a coefficient an order of magnitude lower (the coefficient of pressure drag for the model at the highest speed tested here plus an estimate of skin friction from data cited by Hoerner, 1965) increases their value $10^{0.5}$ times, to 11 $m \cdot s^{-1}$.

Beyond that, the evidence is mainly anecdotal. Alexander (1977) notes without disparagement claims of swimming speeds up to 8 $m \cdot s^{-1}$. Lane (1960) mentions reports of squid leaving the water vertically and clearing deck railings 4.5 to 6 m above a calm sea. Assuming gravitational deceleration only, these heights imply exit speeds of 9.5 to 11 $m \cdot s^{-1}$. Arata (1954) notes an airborne trajectory about 2 m in height and 14 m horizontally; ignoring drag and assuming a normal ballistic trajectory gives an exit speed of about 12 $m \cdot s^{-1}$. Both of these simple calculations, though, may give overestimates: not only do they ignore drag and lift (minor matters for a squid in air) but they neglect the possibility that the last jet of water may be ejected while the squid is in air. And the latter certainly occurs—the photographs of Cole and Gilbert (1970) show that acceleration can continue while an animal is airborne.

In short, it seems reasonably certain that a squid can generate refilling pressures of around 1200 Pa. Similarly, it appears that a squid, pursued by a predatory fish, can achieve speeds in the range of 5 to 10 $m \cdot s^{-1}$. The present study indicates that the net pressure coefficient available for flow-induced refilling is about 0.25. Figure 2 uses

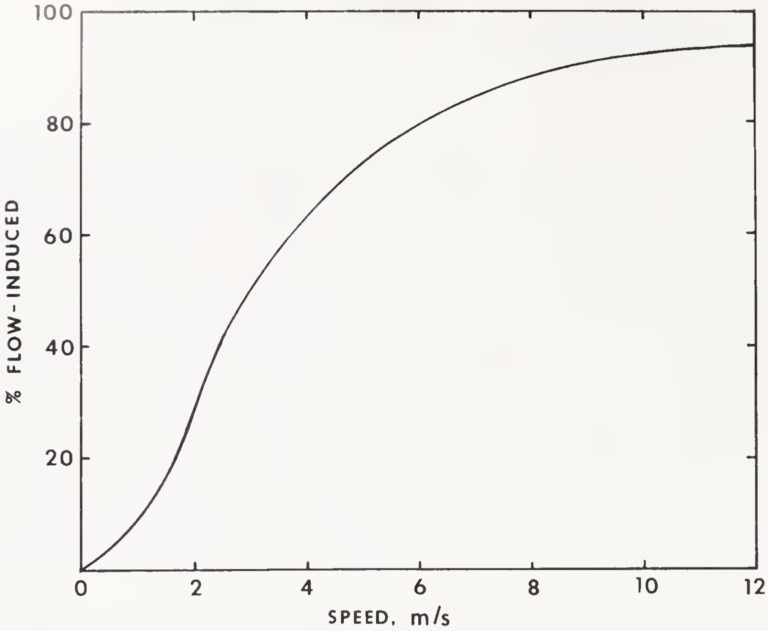

FIGURE 2. The relative contribution of flow-induced pressure differences to total pressure available for refilling as a function of rearward swimming speed, based on present data.

this datum to estimate the relative contribution of hydrodynamics to refilling as a function of swimming speed.

It appears that flow-induced pressure accounts for between 50 and 90% of the total pressure available for refilling in squid during rapid repetitive jetting. Thus the phenomenon is a substantial one. It should permit both more rapid refilling and a greater overall inflation of the mantle cavity and hence a greater maximum swimming speed. It has the virtue of being increasingly effective as speed increases and will be at its best near full inflation, where elastic recoil is minimal and radial muscles have already shortened considerably. It is unlikely, though, that a squid can save energy through the use of flow-induced pressures. Any force that pulls the mantle outward and contributes to refilling is a force against which the circular muscles will have to contend during the expulsion phase, and the distances of mantle movement outward and inward must be the same. But inasmuch as repetitive rearward jetting constitutes an escape response, speed must be far more relevant than any energetic considerations.

The present model is certainly an imperfect squid, although just how imperfect is uncertain in the absense of information on the shape of a squid during repetitive high-speed jetting. Examination of the available data on pressure distribution around streamlined bodies of revolution, though, suggests that a detailed investigation of the effects of taper, size of gap between mantle margin and head, and head size is not warranted. Graphs of pressure coefficients *versus* location simply don't vary much with either the details of shape or, over a very wide range, the Reynolds number. (The present data span a range of Reynolds numbers from 155,000 to 1,350,000.) Arnstein and Klemperer (1936) give a curve similar to the present data for a full-size airship for which the Reynolds number, based on length, was over $10^8$. Goldstein (1938)

(Fig. 215a) presents data at Re = $3 \times 10^6$ especially similar to the present results. Data for a model of the alga, *Halosaccion,* at Re = 14,000 (Vogel and Loudon, 1985), are similar as well, as are data obtained using a toy water rocket (Park Plastics Co., Linden, New Jersey) whose fins had been removed at Re = $10^5$. Minimum pressure coefficients range only from −0.15 to −0.2. The main consistant variation is that the location of the minimum is further downstream for shapes with less blunt upstream ends. Thus the indifference of the present model to alterations in shape comes as little surprise. And, while a squid of about 0.2 m in length was assumed in calculating equivalent swimming speeds in water, the pressure coefficients vary so little with Reynolds number that the data should apply about as well over a considerable size range.

Other, more serious limitations of the present study ought to be borne in mind. Measurements were carried out in steady flow, whereas jetting is an unsteady motion (*sensu* Daniel, 1984). And the act of refilling will to some unknown extent relieve the predicted pressure differences. The major uncertainty, though, comes from the lack of data on actual swimming speeds; since flow-induced pressure is approximately proportional to the square of speed, mere refinement of model and experimental conditions would be of limited usefulness in the absence of better information on swimming speeds in nature.

Nevertheless it is difficult to imagine how substantial flow-induced pressures can be avoided. Indeed, at least one other structural feature of squid is consistent with the occurrence of such pressures during rapid, rearward jetting. The pen more nearly encircles the mantle near the upstream (dorsal) end, where flow will generate compressive forces (positive pressure coefficients in Fig. 1), and thus perhaps provides a measure of compression resistance in a manner analogous to the skull of a fish.

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